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COLLECTION

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HOW THE PRIMITIVE ANTS OF AUSTRALIA START THEIR COLONIES[1]

THE great naturalist and physicist, Réaumur, was the first to attempt an investigation of the founding of colonies among ants, in 1743. Since that time the problem has become more complicated and we now know that these insects practice at least four different methods of colony-founding. Three of these have been satisfactorily elucidated within the past thirty years. A year ago I was able to detect a fourth, quite unexpected method in several Australian species of the very archaic and primitive subfamily Ponerinæ. All four methods represent so many peculiarities in the behavior pattern of the young, recently fecundated female or queen, and these in turn depend on the amount of her food-reserves in the form of adipose tissue and wing-musculature. Species in which these reserves are deficient are compelled to adopt one of two *dependent* methods of colony formation: the young fecundated queen either leaves the maternal colony accompanied by a band of workers that assist her in establishing a new nest and community or she becomes parasitic in a colony of an alien species. The former method is a kind of swarming analogous to that of the honey-bee, but differs in being practiced by the young queens instead of by the old mother queen of the colony. The parasitic ants are of unusual interest, but I shall consider only the two remaining methods, which are of the *independent* type.

[1] Read at the meeting of the National Academy of Sciences, University of Michigan, on November 15, 1932.

Nearly all our ants belong to the four most recent and most specialized taxonomic subfamilies (Myrmicinæ, Pseudomyrminæ, Dolichoderinæ and Formicinæ) and found their colonies in the following manner: After fecundation by the male during her marriage flight, the large-bodied queen, which has been plentifully supplied with abdominal fat during her larval life, descends to the earth, discards her wings, and immures herself completely in a small cell in the soil, under a stone or under the bark of a log. The voluminous wing musculature in her thorax, now useless for purposes of flight, at once begins to break down and dissolve in the blood, so that its proteins, together with the fat in the abdomen, can be used as food by her developing ovaries. These food-reserves enable her not only to mature a number of eggs but also to rear some of the resulting larvæ as a small initial brood of diminutive workers. During this period, which may extend to eight months or even more than a year, she manages to live exclusively on her own tissue-reserves and to feed her larvae with saliva. She also normally devours many of her own eggs and larvae or feeds them to their sister larvae. She often concentrates her care on one or a few of her offspring, so that these pupate and emerge as minute workers before the others. As soon as they are thoroughly mature they break out of the cell and secure food for themselves, their famished mother and the still undeveloped portion of the first brood. They now take over the control of the colony, provide all the food for the diminutive community and thus enable the queen to specialize henceforth as a mere egg-laying machine that supplies them with successive broods to rear. They begin to expand the nest by excavating additional cells and galleries and the colony grows apace, till its trophic status is so favorable that after a few years it can produce males and

young queens. This method of colony formation I have called the *perfectly claustral method.*

I find that the Ponerinae present a very significant variant of this form of colony-founding behavior. More than thirty years ago I showed that these ants do not feed their larvae with liquids by regurgitation, but in a much more primitive fashion, with pieces of freshly killed insects. In all the intervening years I have sought their method of colony-founding, but in vain, and other myrmecologists have had no better success. While accompanying the Harvard expedition to Australia, which has the most superb Ponerine fauna of any continent, I succeeded in filling this gap in our knowledge. The richness of the Australian Ponerine fauna is shown by the fact that at least 300, or 25 per cent., of the 1,200 species, subspecies and varieties of ants now known from the island continent belong to this subfamily. From the United States, which has about the same area as Australia, some 500 species, subspecies and varieties of Formicidae have been described, but only 24 species, or less than 5 per cent., are Ponerinae. In the Palearctic Region the percentage of these ants is certainly no greater, and even in the Neotropical and Paleotropical Regions they probably comprise less than 10 per cent. of the entire ant-fauna.

About a third of the Australian Ponerinae, or 100 species, belong to the genus Myrmecia, which occurs on no other continent. These are the famous "bulldog ants," some of them more than an inch in length, singularly alert, wasp-like, large-eyed, long-jawed and fiercely stinging creatures, which, apart from the poisonous snakes, are really the only formidable animals in the Australian bush. They are evidently a very ancient, Mesozoic group, which bear about the same relation to other ants that the Marsupials bear to the Placental Mammals. A closely allied fossil

genus, Prionomyrmex, is known from the Baltic amber, which is of Lower Oligocene age. The larvae of Myrmecia are very primitive and are fed with pieces of freshly killed insects, though the adults seem to feed exclusively on nectar and sap. Many of the species are beautifully colored. *M. tarsata* F. Smith, *e.g.*, which is nearly an inch long, is beautiful cyan blue, with an orange-tipped abdomen. Some of the species when disturbed hop about like small grasshoppers. There are great differences in the structure of the mandibles, but the subgenera based on these appendages seem to be invalid. They are quite simple in one species, *Promyrmecia aberrans* Forel, which I found in New South Wales in 1914. It is the most primitive and archaic of all known ants and might, therefore, be compared with Ornithorhynchus among mammals. Its colonies consist of not more than a dozen individuals. Its nest, a small hole in dry soil, leads into a perpendicular gallery, about 14 inches long, terminating in a small chamber. The larger species of Myrmecia, however, build mound nests which may be from 1 to 5 feet in diameter, but their population is small and rarely exceeds 150 to 200 individuals.

Now the queens of the Ponerinae, unlike those of the higher ants, are but slightly larger than the workers, and their thorax and abdomen contain only a small amount of musculature and fat. They might be expected, therefore, to found their colonies by swarming, as I thought probable in 1900. This is not the case, however, as I have found in several species of Myrmecia, and in certain species of Amblyopone and Lobopelta in the magnificent Eucalyptus forests of the extreme southwestern corner of Australia. All these ants adopt the same method of colony formation, of which *Myrmecia regularis* may serve as a paradigm. The queen, after fecundation

and deälation in the early months of the year, excavates a large flat cell under a stone and near its periphery, and closes herself off completely from the outside world. She also excavates from the floor of the chamber a gallery extending for some distance into the soil and terminating in a small pocket. This is a retreat, to which she can resort for warmth or for concealment at the slightest disturbance. She does not, however, like the queens of the higher ants, remain rigidly confined to this nest, but, from time to time, breaks through the peripheral wall and forages for food in the open. In November and December (the Australian summer) she starts her brood by laying a number of eggs, which are nearly spherical and are scattered on the floor of the flat upper chamber and not kept in a packet, like the eggs of the higher ants, because she seems to have no salivary secretion with which to glue them together. As soon as the young larvae hatch she leaves the chamber from time to time to capture insects with which to feed them. Both after leaving and after returning to the nest she carefully closes the passageway which she has made in the peripheral wall. Except for her occasional foraging excursions to obtain food for herself or her progeny, the queen's subsequent behavior in rearing the brood is like that of the higher ants.

The independent colony-founding procedure of the Ponerinae may therefore be designated as an *imperfectly,* or *intermittently claustral method.* It is of considerable interest for three reasons: first, being essentially like the method employed by the social wasps (*e.g.,* by our hornets and yellow-jackets of the genus Vespa), it confirms our conviction, reached from many morphological and taxonomic considerations, that the ants are merely a peculiar group of social Vespoids. Second, this intermittent method of colony-founding suggests that the perfectly claustral

method of the higher ants is a late, derivative and highly specialized form of behavior due to the queen's endowment with a considerable accumulation of tissue-reserves and her ability to feed her brood with salivary secretions. And third, the fact that the intermittent is the prevailing and perhaps the only method of colony-founding among the Ponerinae, which are unanimously regarded as the ancestors of the other seven taxonomic subdivisions of ants, supports the theory that the haplometrotic, or single-mother-family, rather than the pleometrotic, or multiple-mother-family, is the phylogenetic basis of all the diverse societies encountered among the hymenopterous insects.[2]

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[2] For a detailed account of the Ponerine method of colony-founding see my forthcoming book, "Colony-Founding among Ants," Harvard University Press, 1933.